

## History and Present Status of the Northern Elephant Seal Population

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**ABSTRACT.** The northern elephant seal, *Mirounga angustirostris*, was presumed extinct by 1892 owing primarily to commercial harvesting for their blubber oil that began in the early 1800s. A small, residual breeding colony survived, however, and with legal protection from further hunting, it grew rapidly through the early 1900s. Immigrants steadily colonized other island and mainland sites in Baja California and California so that by 1991 seals were breeding on fifteen islands and at three mainland beaches. Sixty-four percent of 28,164 northern elephant seal pups born in 1991 were produced on two southern California Channel Islands, San Miguel and San Nicolas. The entire elephant seal population was estimated to number around 127,000 in 1991 and was apparently still increasing by more than 6% annually. The remarkable demographic vitality and sustained population increase of northern elephant seals has evidently been unaffected by the species' low genetic variability and contrasts with recent declines of some populations of the more genetically polymorphic southern elephant seal, *M. leonina*.

*Few, if any, living species today have been so deeply scored, so driven to the very brink of extermination—L. M. Huey (1930)*

Numerous terrestrial and marine species, like the northern elephant seal, experienced great population reductions in the nineteenth and twentieth centuries. But the single remarkable fact about the history of the northern elephant seal population is that despite only narrowly averting extinction, it rebounded with an unparalleled, century-long period of exponential increase (see, e.g., Reeves, Stewart, and Leatherwood 1992 and McCullough and Barrett 1992 for reviews of trends in pinnipeds and other vertebrates). Here we briefly review the population reduction and document its impressive recovery. We focus on number of births as an index of growth during the past three decades and estimate current population size.

## PREHISTORY

Northern elephant seals lived in California waters by the late Pleistocene, evidently derived from monachine ancestors (*Callophoca* group) that entered the Pacific Ocean from the Caribbean through the Central American Seaway in the early Pliocene (Hendey 1972; Barnes and Mitchell 1975; Repenning, Ray, and Grigorescu 1979; de Muizon 1982). Little is known about their distribution during the Pleistocene when dynamic eustatic changes (Orr 1967; Vedder and Howell 1980) both greatly increased and decreased shoreline habitat available to pinnipeds, but archaeological remains show that elephant seals were in southern California waters when humans colonized the region over 15,000 years ago (e.g., Walker and Craig 1979; Snethkamp 1987; Bleitz 1993). Relatively large numbers of aboriginals lived on most of the California islands through the early nineteenth century, using the diverse marine resources on and near the islands for food, clothing, and housing; elephant seals and other pinnipeds were particularly important to aboriginal subsistence (Meighan 1959; Reimann 1964; Glassow 1980; Stewart et al. 1993).

## COMMERCIAL EXPLOITATION

Elephant seal, sea otter, whale, and fur seal hunters operated on and around the California islands from the early 1800s through the 1860s (Scammon 1870, 1874; Ogden 1933, 1941), but they left few records of northern elephant seal harvests. By 1850, northern elephant seals were scarce (Scammon 1870, 1874); it was not until 1866 that northern and southern elephant seals were scientifically recognized as taxonomically distinct (Gill 1866; but see Stewart and Huber 1993).

What we know to be incontrovertible about northern elephant seals in the early and mid-1800s is the following. Their distribution and abundance prior to 1840 is unknown. A few northern elephant seals were killed by sealers at Islas Los Coronados in 1840 and 1846, at Santa Barbara Island in May 1841, and at Cedros and Guadalupe islands in 1846 (Busch 1985). Scammon made a disappointing sealing expedition along the California coast in 1852; during a 5-month period he collected about 350 barrels of oil (Scammon 1874), probably the equivalent of around 100 to 200 adult elephant seals (see Busch 1985). Another 10-month expedition in 1857 met with even less success. Between 1865 and 1880, only a few elephant seals were reported at Isla de Guadalupe and Islas San Benito. Because all were killed as they were encountered, the species was considered extinct by the late 1870s (Townsend 1885). But in 1880, a small herd was discovered on the Baja California mainland south of Isla Cedros, at Bahia San Cristobal (fig. 2.1). Over the next four years, all 335 seals that were seen were killed by

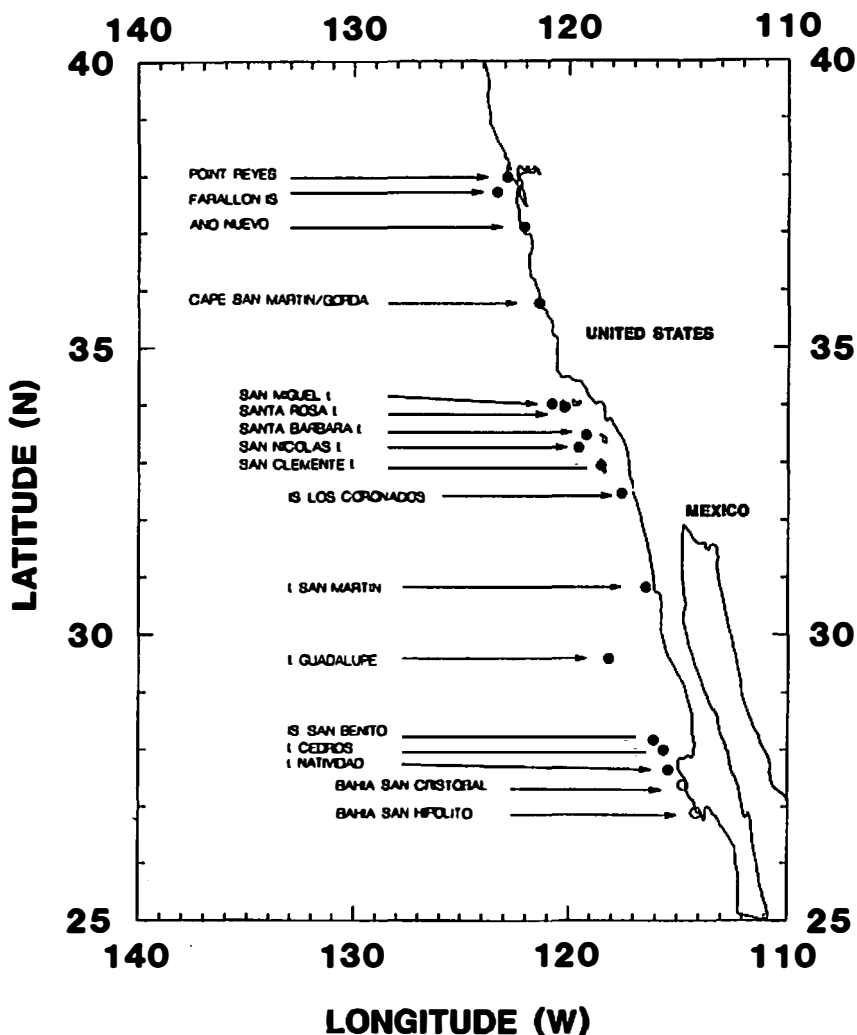


Fig. 2.1. Location of northern elephant seal colonies in 1991 (closed circles) and other alleged historical rookeries (open circles) in U.S. and Mexican waters.

the crews of six ships that visited the beach regularly, mostly in autumn. Three years later, in 1883, 80 elephant seals were found and killed at Isla de Guadalupe, and 4 were killed there in 1884. The species was again considered extinct, and no elephant seals were seen until May 1892, when C. H. Townsend and A. W. Anthony discovered 9 at Isla de Guadalupe; 7 of them were killed for the Smithsonian's museum collection (Townsend 1912; Anthony 1924). "This action was considered justifiable at the time, as the

species was considered doomed to extinction by way of the sealer's trypot and few if any specimens were to be found in the museums of North America" (Anthony 1924: 146). The species was again presumed extinct, for the third time. But small numbers continued to show up at Isla de Guadalupe through 1911, and museum collectors continued to kill them: 4 in 1904 (Townsend 1912) and 14 of 40 on May 26, 1907. "This was a severe stroke dealt to a struggling species, but the appetite of science must be satisfied" (Huey 1930: 189). Townsend returned to Isla de Guadalupe on March 2, 1911, and killed 10 more seals but this time left 125 alive on the beach; on his return voyage to San Diego he searched for elephant seals at Bahia San Cristobal, Islas San Benito, and Isla Cedros but found none (Townsend 1912).

G. A. Bartholomew and C. L. Hubbs (1960), based on their interpretations of published counts of seals from the early 1900s, estimated that the total population in 1890 numbered fewer than 100 animals and speculated that it may have been as small as 20. The actual number of elephant seals that were present during the population bottleneck (or bottlenecks) in the 1800s and early 1900s is unknown because of the following flaws in sightings reports: (1) in most cases, the dates of sightings were not reported; (2) many sightings for which dates were provided were during the nonbreeding season; and (3) the age and sex composition of the seals observed was not determined. This information is vital because the number of seals on land, as well as the composition with respect to age and sex, varies greatly with time of year (Bartholomew 1951; Le Boeuf and Bonnell 1980; Stewart 1989). For example, when Townsend (1912) visited Isla de Guadalupe on March 2, 1911, and left 125 seals alive, it would have been at the end of the breeding season. At this time, some adult males should have been present, but nearly all females should already have returned to sea, leaving their weaned pups behind. Townsend noted that the herd consisted mostly of large males and immature animals of various sizes but that there were more than 15 adult females and 6 newborn young present. The photographs he took, however, show that most of the other "immature" seals were weaned pups, and it is likely that most of the seals ashore were actually molted pups-of-the-year (i.e., about 2 months old). He, like other early authors, also concluded erroneously that early March was the beginning of the breeding season, rather than the end, which emphasizes just how little was known about the natural history of elephant seals before George Bartholomew began his pioneering work on the species in the 1940s (e.g., Bartholomew 1952).

Regardless of whether the bottleneck population numbered in the tens or perhaps low hundreds, the important point is that the thousands of elephant seals alive today are all descendants of that small remnant herd.

## INITIAL RECOVERY: 1900-1965

Northern elephant seals bred only at Isla de Guadalupe from the late 1890s through the 1920s. The colony grew steadily, despite sporadic poaching and scientific collecting (Bartholomew and Hubbs 1960). That early period of increase was chronicled by W. Rothschild (1908, 1910), C. M. Harris (1909), C. H. Townsend (1912), A. W. Anthony (1924) and L. M. Huey (1924, 1925, 1927, 1930) and thoroughly reviewed by Bartholomew and Hubbs (1960). On July 12, 1922, when mostly adult males were ashore molting, 264 seals were counted; a few months later, the Mexican government declared Isla de Guadalupe a biological reserve, and the seals were afforded protection from harassment and poaching (Hanna 1925). From that time on, elephant seals expanded their range; K. W. Radford, R. T. Orr, and C. L. Hubbs (1965) reviewed observations of seasonal migrants during the early 1900s along the coast from San Diego to southeastern Alaska. Other sightings were reviewed by Bartholomew and Hubbs (1960); seals were first seen on Islas San Benito in 1918, San Miguel Island in 1925, Los Coronados and Santa Barbara Island in 1948, San Nicolas Island in 1949, and Año Nuevo Island in 1955. Breeding evidently began in the 1930s at Islas San Benito, in the early 1950s at San Miguel, San Nicolas, and Santa Barbara islands (Bartholomew and Boolootian 1960; Odell 1974; Stewart 1989), and in 1961 at Año Nuevo Island (Radford, Orr, and Hubbs 1965).

From published and available unpublished counts, Bartholomew and Hubbs (1960) estimated that the total population numbered approximately 13,000 in 1957 and approximately 15,000 in 1960, with about 91% of the population residing at Isla de Guadalupe, 8% at Islas San Benito, and 1% on the Channel Islands.

## RECENT TRENDS AND PRESENT STATUS: 1965-1991

Documentation of the population's recovery improved as more became known of the seasonal patterns of terrestrial abundance in the 1950s and 1960s. Table 2.1 lists births at each rookery from 1958 through 1991. The methods used varied slightly among colonies (see appendix 2.1), but all yielded estimates of births either from combined direct counts of suckling, weaned, and dead pups or derived from corrected counts of adult females made during peak breeding season (late January). Most pup counts were made on foot in February, after most births had occurred but before pups had left the rookeries. Some Mexican beaches with difficult access were surveyed from boats. The data for the three islands of Islas San Benito are combined in table 2.1 because of their closeness to each other; data for Año

TABLE 2.1 Northern elephant seal births at California and Mexico rookeries.

	Mexico					California								
	IN	IC	ISB	IG	ILC	SCLJ	SBI	SNI	SMI	SRI	SMG	AN	SFAR	PR
1958									84 <sup>a, b</sup>					
1959								48 <sup>a</sup>				12 <sup>c</sup>		
1961												23 <sup>c</sup>		
1962												32 <sup>c</sup>		
1963												60 <sup>c</sup>		
1964							11 <sup>d, b</sup>	83 <sup>d, b</sup>	878 <sup>d, b</sup>			75 <sup>h</sup>		
1965	0 <sup>i</sup>		800 <sup>i</sup>	3,668 <sup>i</sup>								100 <sup>h</sup>		
1966								136 <sup>c</sup>				143 <sup>h</sup>		
1967												188 <sup>i</sup>		
1968								171 <sup>i</sup>	1,624 <sup>g</sup>			247 <sup>i</sup>		
1969				7,104 <sup>a</sup>				193 <sup>j</sup>				301 <sup>i</sup>		
1970	49 <sup>g</sup>		1,578 <sup>a</sup>	5,520 <sup>a</sup>				210 <sup>i</sup>				310 <sup>i</sup>		
1971					9 <sup>i</sup>			354 <sup>j</sup>				367 <sup>i</sup>	1 <sup>i</sup>	
1972					6 <sup>i</sup>	0 <sup>k</sup>	28 <sup>k, b</sup>	428 <sup>k, b</sup>	2,482 <sup>g</sup>			395 <sup>i</sup>	2 <sup>i</sup>	
1973					18 <sup>i</sup>				3,088 <sup>g</sup>			480 <sup>i</sup>	17 <sup>m</sup>	
1974					28 <sup>i</sup>							605 <sup>i, n</sup>	35 <sup>m</sup>	
1975			815 <sup>a</sup>	6,058 <sup>a</sup>	34 <sup>i</sup>				3,547 <sup>g</sup>			690 <sup>a, n</sup>	60 <sup>m</sup>	
1976									4,014 <sup>g</sup>			814 <sup>q</sup>	104 <sup>m</sup>	
1977			1,359 <sup>a</sup>	5,642 <sup>a</sup>		1 <sup>p</sup>	74 <sup>c</sup>	693 <sup>o</sup>	4,760 <sup>g</sup>			994 <sup>q</sup>	133 <sup>m</sup>	
1978	12 <sup>s</sup>	112 <sup>s</sup>	1,727 <sup>a</sup>	5,552 <sup>a</sup>	45 <sup>i</sup>				5,447 <sup>g</sup>			1,173 <sup>q</sup>	184 <sup>m</sup>	
1979									5,531 <sup>b</sup>	0 <sup>b</sup>		1,353 <sup>q</sup>	232 <sup>m</sup>	1 <sup>c</sup>
1980			1,752 <sup>a</sup>	5,011 <sup>a</sup>				1,187 <sup>r</sup>	6,475 <sup>b</sup>	0 <sup>b</sup>		1,225 <sup>q</sup>	292 <sup>m</sup>	
1981					58 <sup>o</sup>			1,546 <sup>r</sup>	7,272 <sup>b</sup>	0 <sup>b</sup>	3 <sup>u</sup>	1,469 <sup>q</sup>	367 <sup>m</sup>	1 <sup>c</sup>
1982				4,760 <sup>a</sup>		5 <sup>b</sup>		2,312 <sup>r</sup>	7,376 <sup>b</sup>	0 <sup>b</sup>	18 <sup>u</sup>			

1983		0 <sup>b</sup>	25 <sup>b</sup>	1,906 <sup>b</sup>	8,301 <sup>b</sup>	0 <sup>b</sup>	7 <sup>a</sup>	1,566 <sup>a</sup>	475 <sup>m</sup>	2 <sup>i</sup>
1984		3 <sup>b</sup>	80 <sup>b</sup>	2,074 <sup>b</sup>	9,342 <sup>b</sup>	0 <sup>b</sup>	25 <sup>a</sup>	1,685 <sup>a</sup>	447 <sup>z</sup>	12 <sup>i</sup>
1985	166 <sup>7</sup>	49 <sup>6</sup>	97 <sup>b</sup>	2,583 <sup>b</sup>	10,459 <sup>b</sup>	2 <sup>v</sup>	24 <sup>a</sup>	1,701 <sup>a</sup>	360 <sup>z</sup>	15 <sup>i</sup>
1986		53 <sup>6</sup>	73 <sup>b</sup>	2,626 <sup>b</sup>	9,824 <sup>b</sup>	0 <sup>b</sup>	4 <sup>a</sup>	1,742 <sup>a</sup>	434 <sup>z</sup>	19 <sup>i</sup>
1987		1 <sup>b</sup>		2,835 <sup>b</sup>	10,120 <sup>b</sup>	2 <sup>b</sup>	13 <sup>a</sup>	1,524 <sup>a</sup>	395 <sup>y</sup>	20 <sup>i</sup>
1988	227 <sup>8</sup>			3,366 <sup>w</sup>	11,035 <sup>w</sup>	2 <sup>w</sup>	13 <sup>a</sup>	1,725 <sup>s</sup>	393 <sup>y</sup>	34 <sup>i</sup>
1989				4,466 <sup>w</sup>	11,079 <sup>w</sup>	3 <sup>w</sup>	67 <sup>a</sup>	2,001 <sup>s</sup>	380 <sup>y</sup>	44 <sup>i</sup>
1990		64 <sup>8</sup>		4,101 <sup>w</sup>	12,152 <sup>w</sup>	27 <sup>w</sup>	65 <sup>a</sup>	1,986 <sup>s</sup>	396 <sup>y</sup>	52 <sup>z</sup>
1991	391 <sup>2</sup>	1,662+2	4,962 <sup>2</sup>	4,082 <sup>w</sup>	13,884 <sup>w</sup>	73 <sup>w</sup>	263 <sup>a</sup>	2,248 <sup>s</sup>	352 <sup>y</sup>	81 <sup>z</sup>

COLONY ABBREVIATIONS: Isla Natividad (IN), Isla Cedros (IC), Islas San Benito (ISB), Isla de Guadalupe (IG), Islas Los Coronados (ILC), San Clemente Island (SCL), Santa Barbara Island (SBI), San Nicolas Island (SNI), San Miguel Island (SMI), Santa Rosa Island (SRI), Cape San Martin/Gorda (SMG), Año Nuevo Island and Mainland (AN), South Farallon Islands (SFAR), Point Reyes Headlands (PR).

SOURCES OF DATA: *Mexico rookeries*: <sup>1</sup>Rice, Kenyon, and Lulich B. 1965; <sup>2</sup>J. P. Gallo-Reynoso and A. Figueroa-Carranza, unpubl. data; <sup>3</sup>Le Boeuf, Countryman, and Hubbs 1975; <sup>4</sup>Antonelis, Leatherwood, and Odell 1981; <sup>5</sup>Le Boeuf and Mate 1978; <sup>6</sup>B. S. Stewart, unpubl. data; <sup>7</sup>K. Connally, pers. comm.; <sup>8</sup>W. T. Everett, pers. comm. *California rookeries*: <sup>a</sup>Bartholomew and Boolootian 1960; <sup>b</sup>Stewart 1989; <sup>c</sup>Orr and Poulter 1965; <sup>d</sup>Odell 1971; <sup>e</sup>Klopfer and Gilbert 1966; <sup>f</sup>Peterson, Gentry, and Le Boeuf 1968; <sup>g</sup>R. L. DeLong, unpubl. data; <sup>h</sup>Poulter and Jennings 1966; <sup>i</sup>Le Boeuf and Briggs 1977; <sup>j</sup>Odell 1974; <sup>k</sup>Antonelis, Leatherwood, and Odell 1981; <sup>l</sup>Le Boeuf, Ainley, and Lewis 1974; <sup>m</sup>Huber 1987; <sup>n</sup>Le Boeuf and Panken 1977; <sup>o</sup>Le Boeuf and Bonnell 1980; <sup>p</sup>Le Boeuf and Mate 1978; <sup>q</sup>Le Boeuf and Reiter 1991; <sup>r</sup>Stewart and Yochem 1984; <sup>s</sup>Le Boeuf and colleagues, unpubl. data; <sup>t</sup>Allen, Peaslee, and Huber 1989; <sup>u</sup>R. Jameson, unpubl. data; <sup>v</sup>Stewart and Yochem 1986; <sup>w</sup>Stewart 1992; <sup>x</sup>Huber et al. 1991; <sup>y</sup>W. Sydeman, unpubl. data; <sup>z</sup>S. G. Allen, unpubl. data.

Nuevo Island and Año Nuevo mainland are combined for the same reason. From the data in table 2.1, we conclude the following.

The total elephant seal population, as reflected by births, increased 6.3% annually (= finite rate of increase,  $\lambda$ , where  $\lambda = e^r$ ; see appendix 2.2) from 1965 through 1991 ( $r = .061$ ;  $R^2$ , the coefficient of determination = .947;  $p$ , the significance of slope  $\neq 0$ ,  $< .001$ ; see appendix 2.2). C. F. Cooper and B. S. Stewart (1983) calculated its increase at 8.3% from 1965 through 1977. The lower rate that we calculated here for the entire period (1965–1991) is evidently due to the lack of any apparent increase in Mexico since 1970. Growth of the total population from 1965 through 1991 was due primarily to growth at California rookeries, where births increased 14.1% annually ( $r = .132$ ,  $R^2 = .901$ ,  $p < .001$ ), only slightly less than from 1965 through 1982 ( $\lambda = 1.145$ ; Cooper and Stewart 1983).

Births increased slightly in Mexico between 1965 and 1970 but have not changed since then (fig. 2.2; slope of regression of births on time = 0,  $p = .903$ ; see appendix 2.2). D. W. Rice, K. W. Kenyon, and D. L. Luch B. (1965) suggested that carrying capacity of the Isla de Guadalupe rookery was reached by 1960. Counts made since then at the largest breeding beaches at Isla de Guadalupe support that conclusion; virtually all breeding space is now occupied and crowded during peak breeding season (J. P. Gallo-Reynoso and A. Figueroa-Carranza, unpubl. data). Because there are few recent counts at Islas San Benito, the trends on these islands are less clear (table 2.1). However, surveys of the central island (the easiest of the three to census and the site at which the data are most complete) show steady growth since 1970 (B. J. Le Boeuf, unpubl. data; B. S. Stewart, unpubl. data; J. P. Gallo-Reynoso and A. Figueroa-Carranza, unpubl. data). Births almost tripled from the early to mid-1970s (table 2.1). The central island accounted for 28.1, 37.2, and 45.1% of births on the entire island group in 1970, 1977, and 1980, respectively. If we assume that the 1,666 pups produced on the central island in 1991 accounted for 37% of the total pup production in that year, then the rookery produced 4,500 pups in 1991 and the colony is evidently still increasing. This is our tentative conclusion, but we must be guarded about the accuracy of the estimate. Some of the increase of central island numbers may have resulted from movements of seals from the west island where tourist and fishing activities have increased during the past two decades. Despite the increases at Isla Cedros and Islas San Benito, the Mexican population has not changed substantially during the past two decades, evidently because births at Isla de Guadalupe have declined, after peaking in the late 1960s (table 2.1).

The rapid increase in births at San Miguel Island, the largest colony in the species' range, accounts for most of the growth in California. Elephant seals bred only at the western tip of the island in 1968 (Le Boeuf and Bon-



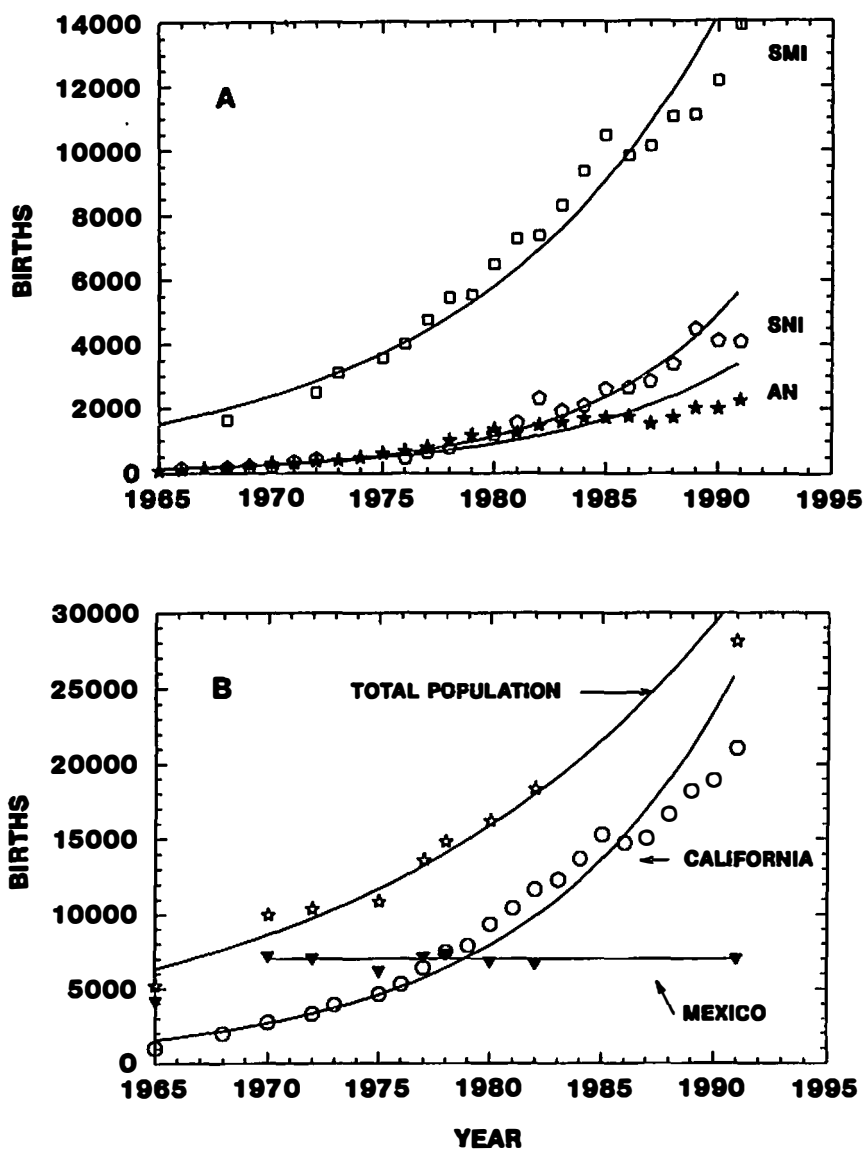


Fig. 2.2. Growth of the northern elephant seal population as reflected by births. (A) Increases in births at San Miguel Island (SMI), San Nicolas Island (SNI), and Año Nuevo Island and mainland combined (AN). (B) Growth of the entire northern elephant seal population, California segment, and Mexican segment. An intense El Niño affected North Pacific waters from late 1982 through 1983 (see text for details of immediate and delayed effects on northern elephant seals).

nell 1980; R. L. DeLong, pers. observ.). In subsequent years, breeding groups appeared farther east, so that by 1980, seals were breeding along the entire southern coast (Stewart 1989, 1992). Some of the northern beaches, however, are unused still. Births increased 9.3% annually ( $r = .089$ ,  $R^2 = .963$ ,  $p < .001$ ) from 1965 through 1991; that growth and the coincident eastward expansion of breeding led to the colonization of Santa Rosa Island in 1985 (Stewart and Yochem 1986). Growth at San Nicolas Island (the second-largest colony), where expansion has followed patterns similar to those at San Miguel Island (Stewart 1989, 1992), has also been rapid ( $\lambda = 1.158$ ,  $r = .147$ ,  $R^2 = .976$ ,  $p < .001$ ). The brief decline in California births in 1985 was evidently due to poor recruitment of pups (owing to poor survival or retarded maturation or both; Huber, Beckham, and Nisbet 1991; Le Bocuf and Reiter 1991; B. S. Stewart, unpubl. data) that were born just before and during the 1982–1983 El Niño Southern Oscillation event. Pregnancy rates declined temporarily at some rookeries in 1984 and 1985 but there is no evidence that adult survival changed as a result of this intense oceanographic perturbation (Huber, Beckham, and Nisbet 1991; Le Bocuf and Reiter 1991).

Many new colonies formed in the last three decades, including at least three in Mexico. Elephant seals have clearly established breeding colonies on Isla Cedros and Islas Los Coronados. Births increased eightfold at Isla Cedros, an island that could sustain many more seals. Breeding space is limited on Islas Los Coronados, so carrying capacity has evidently been reached. Pups have been born on Isla Natividad, but monitoring of this island has been poor. At least two pups were produced on Isla San Martín (not shown in table 2.1) in 1978 (Le Bocuf and Mate 1978), but heavy human traffic on this island may preclude future growth.

California has at least six colonies that were founded since 1960. The San Clemente Island and the Santa Rosa Island colonies are in southern California. The other four colonies are in Central California; Cape San Martín/Gorda and Point Reyes Headlands are on the mainland, the Año Nuevo colony occupies both a small island and the immediate mainland, and the South Farallons colony is on an island (fig. 2.1). Año Nuevo Island reached carrying capacity in the late 1970s with annual production slightly under 1,000 pups. The colonization of Point Reyes Headlands in 1981 (Allen, Peaslee, and Huber 1989) is evidently linked to growth of the Año Nuevo and South Farallon Islands colonies. Births are still increasing at Año Nuevo and at Point Reyes Headlands. The recent explosive increase in births on beaches near Cape San Martín/Gorda is difficult to explain. Pups were first born in the area on a small, steep-backed gravel beach about 1 km north of Cape San Martín in 1981 or perhaps 1980. Breeding was restricted to that exposed site until 1989 when seals abandoned it and be-

gan using a longer gravel beach about 2 km south near Gorda. The better protection of that site against winter storms and surf was evidently more attractive to pregnant females, as indicated by the fourfold increase in births in the past two years (table 2.1).

#### COLONIZATION PROCESS, IMMIGRATION AND EMIGRATION

Births increased rapidly following colonization of all sites (table 2.1, fig. 2.2), and several colonies are still in this incipient growth stage. Immigrants from Isla de Guadalupe almost certainly colonized the other islands in Mexico and those in southern California. Our observation of the movement patterns of tagged seals during the past three decades (Condit and Le Boeuf 1984; B. J. Le Boeuf, unpubl. data; B. S. Stewart, unpubl. data) support that idea and also indicate the following: Año Nuevo was colonized by immigrants from San Miguel Island and to a lesser extent, immigrants from San Nicolas Island; the South Farallon Islands were colonized by immigrants from San Miguel, San Nicolas, and Año Nuevo islands (Le Boeuf, Ainley, and Lewis 1974; Huber et al. 1991). Some rookeries established in the 1980s were colonized by seals from neighboring rookeries. For example, Point Reyes Headlands was initially colonized by seals from the South Farallon Islands and Año Nuevo, and only recently have immigrants from San Miguel and San Nicolas islands been observed there (Allen, Peaslee, and Huber 1989; S. G. Allen, unpubl. data).

Some northern rookeries (e.g., Año Nuevo) in the expanding part of the range apparently still owe their growth more to a high immigration rate than to internal recruitment (which fuels most of the growth at rookeries at San Nicolas and San Miguel islands). Reproductive success of females at Año Nuevo has not been sufficient to account for the increases there (Le Boeuf and Reiter 1988). San Miguel Island seems to be the main source of immigrants. Immigration is also the primary cause of growth at the South Farallon Islands colony (Huber et al. 1991), where immigration rates from Año Nuevo, San Miguel Island, and San Nicolas Island were 3.9, 1.9, and 0.6%, respectively, between 1974 and 1986. These immigration rates were positively correlated with proximity to the South Farallon Islands.

Seals began colonizing new areas before carrying capacities were reached at most natal beaches. For example, Channel Islands colonists began breeding at Año Nuevo Island at least 20 years before San Miguel or San Nicolas Island habitats became crowded (see Orr and Poulter 1965; Stewart 1989, 1992). Similarly, Año Nuevo Island colonists began breeding at the South Farallon Islands and at Año Nuevo mainland 6 to 8 years before the island reached carrying capacity (see Le Boeuf, Ainley, and Lewis 1974; Reiter, Panken, and Le Boeuf 1981; Le Boeuf and Reiter 1991).

## TOTAL POPULATION SIZE

The dynamic age structure of the northern elephant seal population (e.g., Huber et al. 1991) hinders accurate predictions of present population size from pup counts or of total seals hauled out at any time. Estimates of births are, however, useful for estimating rate of change in population size, although such calculations have problems (e.g., see Berkson and DeMaster 1985). Despite some obvious shortcomings, we use pup counts as a convenient index of population growth because superior measures of life history parameters are not available for each rookery.

Total population size may be about 3.5 to 4.5 times births (e.g., Hewer 1964; Bonner 1976; Harwood and Prime 1978, Stewart 1989). For comparison with southern elephant seals (Laws, this volume), we use T. S. McCann's formula and multiply births by 3.5 to estimate total population size at the end of the breeding season, exclusive of pups (McCann 1985). From table 2.1, we multiply 3.5 times the 28,164 pups born in 1991 to obtain the estimate of 98,574 elephant seals older than pups in the entire population in 1991. If the young of the year are added to this figure, there were approximately 127,000 elephant seals in existence in early spring 1991.

In 1991, Mexican rookeries contributed 25.5% of all births and California, 74.8%; San Miguel Island alone produced nearly half (49.3%) of all elephant seal pups. The world total of southern elephant seals in 1991 (Laws, this volume) was roughly 6.8 times larger than that of northern elephant seals.

## FUTURE GROWTH

The northern elephant seal has lived in eastern North Pacific waters for at least several hundred thousand years. Their occurrence and apparent vitality in these waters today is remarkable considering their fortuitous emergence in the twentieth century after facing extinction in the nineteenth century. There seem to be few barriers to the species' continued population growth and range expansion. In the immediate future, growth of the population will probably be determined primarily by events on southern California rookeries. Growth at San Nicolas and San Miguel islands will almost certainly slow as the limited remaining habitat becomes occupied and as crowding on those islands constrains reproductive success. The new colony at Santa Rosa Island, however, has substantial breeding beach habitat that could support continued rapid growth in California. Neighboring Santa Cruz Island also offers some additional habitat, although of poorer quality than at Santa Rosa Island. The seals may also continue their northward expansion. They are now hauling out at Cape St. George in northern

California, at Cape Arago in Oregon, and on Vancouver Island in British Columbia. Recent information on seasonal movements and foraging locations of northern elephant seals (see DeLong, Stewart, and Hill 1992; Stewart and DeLong 1993; Stewart and DeLong, this volume; Le Boeuf, this volume) suggests that eventual breeding at these sites is quite plausible.

M. L. Bonnell and R. K. Selander (1974) found that northern elephant seals were homozygous at 23 loci coding for 20 blood allozymes and suggested that this was due to a loss of genetic variability when elephant seals were reduced to small numbers in the 1800s. Recent research on nuclear and mitochondrial DNA (Hoelzel et al. 1991; Lehman, Wayne, and Stewart 1993) reaffirms the earlier findings of low heterozygosity, although these studies revealed greater levels of variability than the electrophoretic analysis of blood allozymes did. Reduced genetic variability may compromise the population viability of some species of mammals (e.g., O'Brien et al. 1985; O'Brien et al. 1987), but many other species have persisted for a long time despite population bottlenecks, founder events, isolation, inbreeding, and low levels of genetic variation (e.g., Gill 1980; Nevo, Beiles, and Ben-Shlomo 1984; Gilbert et al. 1990; Benirschke and Kumamoto 1991; Wayne et al. 1991). A lack of substantial genetic variability has not limited the phenomenal population recovery of northern elephant seals. Indeed, their recovery contrasts ironically with the recent decline of some populations of the closely related southern elephant seal (Laws, this volume), which is genetically more polymorphic (McDermid, Ananthakrishna, and Agar 1972; Hoelzel et al. 1991). The consequences of low genetic variability for future population growth of northern elephant seals are unpredictable.

## APPENDIX 2.1

### *Field Data Collection Methods*

Survey methods differed slightly among rookeries as described below due to differences in colony size, dispersion, and logistical constraints. Nonetheless, our studies produced annual estimates of births and, in most cases, neonatal mortality at each colony.

*San Miguel Island.* Each year in late February two or three people walked among and counted weaned, suckling, and dead pups at all beaches on SMI. Observers' counts of live pups were compared after each relatively small group (<100) was counted; counts usually differed by less than 2%, but if the tallies differed by 5% or more, the group was counted again. In this way an entire cohort of pups distributed along approximately 30 km of shoreline could be surveyed in two or three days.

*San Nicolas Island.* Each breeding season, surveys were made every one to two days at three sites and once each week at all breeding sites along the

35 km of coastline of SNI. Weaned and suckling pups were tallied two or three times during each survey, and dead pups were marked and mapped to ensure that those that died prior to weaning were accounted for but none more than once. The number of births and pup deaths was determined for each breeding site and summed at the end of the season to determine total annual production.

*Santa Rosa Island and Santa Barbara Island.* The numbers of live pups present on SRI and SBI were determined by photographing them during aerial surveys in late January. These counts were corrected to estimate each year's births according to seasonal phenology of births documented by Stewart (1989). Pup mortality was not determined.

*Cape San Martín.* Nursing, weaned, and dead pups were counted periodically in January, February, or early March each year at various small beaches within 2 km of Cape San Martín beginning in 1981. Pre-weaning mortality could not be determined accurately.

*Año Nuevo.* Most estimates of births were derived from daily or weekly counts during the breeding season of all seals present; those counts included dead, suckling, and weaned pups. In some circumstances births were estimated as follows: (1) counts of females present at ANI and ANMI in late January were first adjusted to account for those that had already left the rookeries and for those that had not yet arrived to provide an estimate of the number of females that visited during the breeding season; (2) 98% of the females estimated to have hauled out were assumed to have given birth. Prior to 1980, all or most pups that died were accounted for by removing them from breeding aggregations or marking them with paint or dye. Since 1980, preweaning mortality on the island has been estimated as follows: (1) weaned and suckling pups were counted on March 1 or 2 to yield an estimate of pups weaned for the season; (2) mortality was then derived by subtracting that estimate from an estimate of the number of females that gave birth during the season (as summarized above). Some estimates of births reported here (table 2.1) are corrections of those published earlier.

*South Farallon Islands.* Prior to 1987, births were determined in several ways depending on breeding location at SFAR. Pup carcasses were removed from the nine breeding sites whenever possible. At sites that were not washed by high tides, all deaths were accounted for because all females that gave birth, and their pups, were marked with hair dye. At other sites, observations of a female's appearance (i.e., blood on her hind quarters) or behavior were used to determine if newborn pups had disappeared (and

presumably drowned) undetected during high tides or storms. Weaned pups were counted at the end of the breeding season and added to estimates of records of dead pups to derive an estimate of each season's births.

Beginning in 1987, births at the primary breeding site were determined as follows: (1) a peak count of females was made in late January; (2) based on reproductive characteristics of tagged females observed during the season, 93.2% of the females present during the peak count were assumed to have given birth; and (3) the estimate was adjusted to account for females that had departed already or had not yet arrived. Pup mortality was estimated indirectly by subtracting the number of weaned pups counted in late February from the estimate of births derived from the peak season female count. Births and pup deaths at the other eight breeding sites were determined by monitoring all females that were present and that were uniquely marked with hair dye.

*Point Reyes Headland.* Counts of live and dead pups were made at least weekly from bluffs overlooking beaches along the Point Reyes Headland. Estimates of pup deaths are rough minima because some carcasses probably washed out to sea undetected between observations. Estimates of births were made by adding the peak count of live pups to estimates of deaths that occurred prior to that count.

*Mexican Islands.* Surveys were made opportunistically on foot or from skiffs nearshore from 1968 to 1991 at IG, ISB, IC, and at other small rookeries in Mexico (fig. 2.1, table 2.1). Complete surveys of Isla de Guadalupe's west side were rarely made because of rough island terrain and heavy seas near the coastlines. We report only counts made near the end of the breeding season when nearly all births had occurred but when few pups had departed the rookeries.

## APPENDIX 2.2

### *Analyses of Rates of Change of Elephant Seal Births*

We calculated observed rates of increase ( $r$  = intrinsic rate of increase) in births by linear regression (Zar 1974). We examined the fit of an exponential model,  $\log_e$  number of births regressed on time where  $r$  is the slope of the regression line (Caughley and Birch 1971; Caughley 1977). We present the coefficient of determination ( $= R^2$  to distinguish it from rate of increase) to describe the proportion of the total variation in births that is accounted for by time. For comparative purposes, we convert exponential rates ( $r$ ) to finite rates ( $e^r = \lambda$ ; Caughley 1977: 6). When the exponential model fit poorly, we used a linear model of births regressed on time. For both mod-

els, we present the level of significance ( $p$ ) at which we did (if  $p < .05$ ) or did not (if  $p > .05$ ) reject the null hypothesis that the slope of regressions did not differ from zero.

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